ZooKeys 787: 91–105 (2018)
doi: 10.3897/zookeys.787.28195
http://zookeys.pensoft.net

RESEARCH ARTICLE

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Roisinitermes ebogoensis gen. & sp. n., an outstanding drywood termite with snapping soldiers from Cameroon (Isoptera, Kalotermitidae)

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Academic editor: *P. Stoev* | Received 5 July 2018 | Accepted 27 August 2018 | Published 2 August 2018

http://zoobank.org/C6973DAD-84F4-4C54-87D0-4EDFBEDFF161

Citation: Scheffrahn RH, Bourguignon T, Akama PD, Sillam-Dussès D, Šobotník J (2018) *Roisinitermes ebogoensis* gen. & sp. n., an outstanding drywood termite with snapping soldiers from Cameroon (Isoptera, Kalotermitidae). ZooKeys 787: 91–105. https://doi.org/10.3897/zookeys.787.28195

Abstract

Termites have developed a wide array of defensive mechanisms. One of them is the mandibulate soldier caste that crushes or pierces their enemies. However, in several lineages of Termitinae, soldiers have long and slender mandibles that cannot bite but, instead, snap and deliver powerful strikes to their opponents. Here, we use morphological and molecular evidence to describe *Roisinitermes ebogoensis* Scheffrahn, **gen. & sp. n.** from near Mbalmayo, Cameroon. Soldiers of *R. ebogoensis* are unique among all other kalotermitid soldiers in that they possess snapping mandibles. The imago of *R. ebogoensis* is also easily distinguished from all other Kalotermitidae by the lack of ocelli. Our study reveals a new case of parallel evolution of snapping mandibles in termites, a complex apparatus responsible of one of the fastest biological acceleration rates measured to date.

Keywords

Ethiopian Region, mandibles, ocellus, taxonomy

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Introduction

Termites are extremely abundant (Martius 1994, Eggleton et al. 1996) and colonies may contain millions of individuals attracting a wide variety of predators (Deligne et al. 1981). Additionally, termites experience strong intra- and inter-specific competition (Levings and Adams 1984, Thorne and Haverty 1991). To combat against the plethora of agonistic opponents, termites have developed a rich array of defensive strategies. The most important defenses are expressed in the soldier caste that is ancestral to all extent termites (Roisin 2000).

Soldiers are specialized sterile colony defenders possessing exaggerated morphology of the head and mandibles (Prestwich 1984). One of their most intriguing defenses is exemplified by long and slender snapping mandibles (Deligne et al. 1981). The snapping mandibles are paired with muscles to store potential energy which, when released, delivers a powerful strike producing one of the fastest accelerations known among animals (Seid et al. 2008). All termite species with snapping soldiers described so far belong to the Termitinae (Bourguignon et al. 2017), suggesting that snapping soldiers evolved several times independently within this subfamily. Alternatively, soldiers with snapping mandibles might have evolved once, and independently reverted to a biting strategy in several lineages.

The monophyletic family Kalotermitidae (Inward et al. 2007) constitutes almost half of all "lower termite" genera and species (Krishna et al. 2013) and has fossil records to the mid-Cretaceous (Engel et al. 2009). Kalotermitids live entirely in wood as "one-piece" nesters (Abe 1987) which facilitates transoceanic dispersal (Scheffrahn and Postle 2013). Kalotermitids occur in all ecozones and numerous genera have vast distributions (e.g. *Calcaritermes*, *Cryptotermes*, *Glyptotermes*, *Kalotermes*, *Marginitermes*, *Neotermes*, and *Procryptotermes*). A few species of *Cryptotermes* (Scheffrahn et al. 2009) and *Incisitermes* (James et al. 2013, Yasuda et al. 2003) have also been dispersed by human activity. A few species are major pests of dry wood (Su and Scheffrahn 2000) or minor pests of tree crops (Constantino 2002).

The monumental revision of the Kalotermitidae by Krishna (1961) provided the morphological diagnoses for all extant genera with the exception of the recently described *Longicaputermes* (Ghesini et al. 2014). Aside from *Longicaputermes*, all new kalotermitid species described after Krishna's 1961 revision, ca. 115, have been assigned to one of the 21 genera he recognized. The soldier caste of several genera has unmistakable characters: e.g., the scooped out frons of *Eucryptotermes*, the massive third antennal article of *Marginitermes*, the large ovoid head of *Pterotermes*, or the spur on the fore tibia of *Calcaritermes*. We herein describe a new genus and species of Kalotermitidae, *Roisinitermes ebogoensis*, which possesses equally unmistakable soldiers. The soldier of *R. ebogoensis* is the first outside the Termitinae to have snapping mandibles.

Material and methods

Illustrations and measurements

Images of individuals were taken as multi-layer montages using a Leica M205C stereomicroscope with a Leica DFC 425 module run with Leica Application Suite software version 3. Preserved specimens, stored in 85% ethanol, were positioned in a transparent petri dish filled with Purell hand sanitizer (70% EtOH). Measurements (Tables 1–2) were obtained using an Olympus SZH stereomicroscope fitted with an ocular micrometer. A field photograph of live specimens placed in a small paper-lined Petri dish was taken with a Canon EOS 5DS R combined with a Canon EF 100mm f/2.8L Macro IS USM lens. Morphological terminology follows that of Krishna (1961).

Phylogenetic analyses

DNA was extracted from five individuals of *R. ebogoensis*, after removal of the digestive tract. The full mitochondrial genome was amplified with TaKaRa LA Taq in two long PCR reactions using primers specifically designed for termites (Bourguignon et al. 2016). Long PCR fragments were pooled in equimolar concentration, and 75-bp paired-end reads were obtained using Illumina MiSeq. We subsampled a total of 10,000 reads and assembled the full mitochondrial genome with SPAdes, under default parameters (Bankevich et al. 2012). The total coverage of the assembly was 82-fold.

We used the mitochondrial genomes of ten species of Kalotermitidae, including one sample of *Roisinitermes ebogoensis* sequenced in this study. We used four non-Kalotermitidae termite species as outgroups to root the tree: *Zootermopsis angusticollis*, *Hodotermopsis sjostedti*, *Coptotermes sjostedti*, and *Termitogeton planus*. All mitochondrial genomes, except that of *R. ebogoensis*, have been published recently (Suppl. material 1: Table S1). Each gene of the mitochondrial genome was aligned separately using MAFFT v7.300b with the option "--maxiterate 1000 --globalpair" for higher accuracy. For protein-coding genes, we first aligned genes as protein, then converted protein sequence alignments into the corresponding codon alignments using PAL2NAL (Suyama et al. 2006). The 22 tRNAs and the two ribosomal RNAs were aligned as DNA. The resulting alignments were concatenated with FASTconCAT v1 (Kück and Meusemann 2010). Alignments were separated in five partitions: one for each codon position of the protein-coding genes, one for the combined ribosomal RNA genes, and one for the combined tRNA genes.

We reconstructed phylogenetic trees using Maximum Likelihood and Bayesian approaches. We ran the analyses twice, once with the third codon position included, and once without third codon position. The Bayesian phylogenies were implemented

in MrBayes 3.2 (Ronquist et al. 2012) with unlinked partitions, each of four chains (three hot and one cold). The chain length was of two million generations with sampling every 2000 generations. 800,000 generations were discarded as burnin, to ensure that the chain reached convergence, as determined by Tracer 1.5 (Rambaut and Drummond 2007). We ran two replicates of each analysis to ensure consistency of the results. For each partition of the data, we assigned an independent Generalized Time Reversible model with gamma-distributed rate variation across sites and a proportion of invariable sites (GTR + G +I). The reconstruction of Maximum Likelihood phylogenies was carried out with RAxML (Stamatakis et al. 2008). We used the GTR-GAMMA model of rate heterogeneity across sites. Node support was estimated using 1000 bootstrap replicates.

Results

Phylogenetic analysis

Our phylogenetic analyses supported the monophyly of Kalotermitidae (Figure 1). The four analyses yielded identical tree topologies, with one exception: in the Bayesian analysis without third codon position *Rugitermes* was the sister group of *Neotermes* + *Cryptotermes* + *Incisitermes* + *Roisinitermes*, while in the other three analyses *Rugitermes* + *Neotermes* sp. A formed the sister group of *Neotermes insularis* + *Cryptotermes* + *Incisitermes* + *Roisinitermes*. *Roisinitermes* was consistently placed next to *N. insularis*.

Systematics

***Roisinitermes* Scheffrahn, gen. n.**
http://zoobank.org/9AE40F98-CA9E-45AC-849E-A034F19E8DAE

Type-species. *Roisinitermes ebogoensis* Scheffrahn sp. n.

Winged Imago. Ocelli not visible either by pigmentation or cuticular protrusion (Figure 2A–C). Fore wing with unsclerotized media and cubitus arising from a common vein distal from scale suture; radial sector with 5–6 anterior branches; subcosta very close and difficult to discern from costal margin (Figure 2D). Hind wing with radial sector and cubitus arising from a common vein distal to suture. Tibial spurs 3:3:3; tarsi without arolia. The left imago/nymph mandible with anterior margin of their marginal tooth ca. 1.5 times longer than length of the posterior margin of the first plus second marginal tooth; right mandible with posterior margin of second marginal tooth 1.4 times as long as molar plate (Figure 3).

Diagnosis. The lack of visible ocelli is unique among all other Kalotermitidae. In Krishna's 1961 generic key, *Roisinitermes* would lead to couplet 2 (*Epicalotermes*).

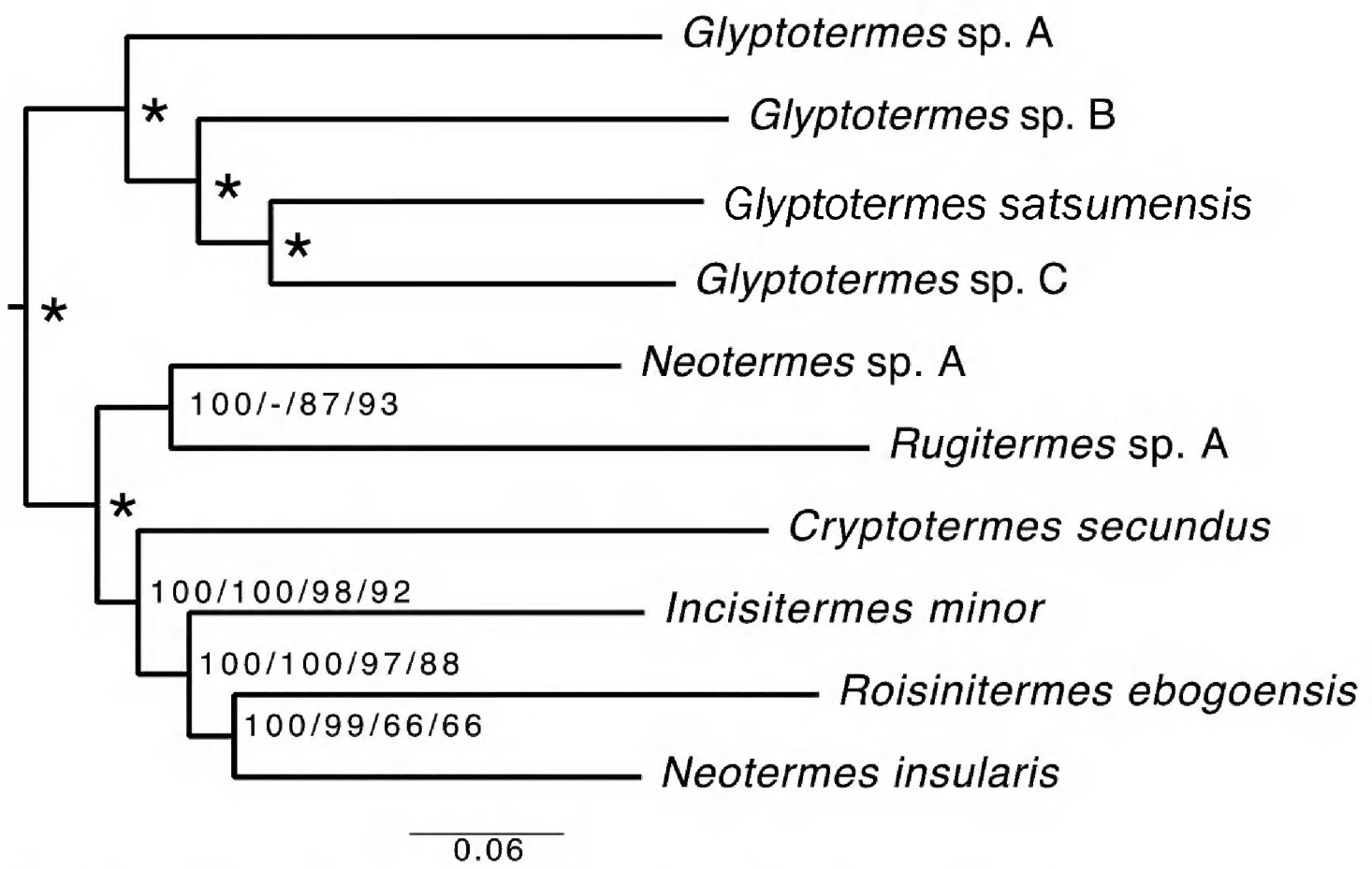

Figure 1. Phylogenetic tree of Kalotermitidae based on full mitochondrial genomes. The tree depicted was reconstructed with RAxML using the data matrix without third codon position. Node labels are the Maximum Likelihood bootstrap supports and the Bayesian posterior probabilities in the following order, from left to right: posterior probability of the analysis with third codon position included, posterior probability of the analysis without third codon position, bootstrap support of the analysis with third codon position included, bootstrap support of the analysis without third codon position, *indicates 100% bootstrap support and 1.0 posterior probability for all four analyses.

Soldier. Monomorphic (Figs 4, 5). Eye spots prominent; large, dark brown. Frons bilobed in dorsal view, crested with rugose longitudinal wrinkles, rugosity below frons oriented longitudinally. Small horn-like projection at terminus of ventral genae. Mandibles sticklike; downward arching in lateral view. Dentition very weak; basal humps project sharply.

Diagnosis. Stick-like mandibles unique among all other kalotermitid soldiers. In Krishna's 1961 key, *Roisinitermes* leads to couplet 17 (*Allotermes*). In dorsal view, the mandibular blades of *Allotermes*, especially *A. denticulatus* Krishna 1962, somewhat resemble those of *Roisinitermes* as those of the former are long, rather narrow and with rudimentary dentition. In lateral view, however, the *Roisinititermes* mandibles differ from all other kalotermitids with projecting mandibles in that the *Roisinitermes* mandibles arch downward. Although the *Roisinitermes* imago venation and dentition is very similar to those of *Epicalotermes*, the soldier of *Roisinitermes* shares no major characters with the *Epicalotermes* soldier.

Etymology. The genus is named in honor of Dr. Yves Roisin for his many contributions to the study of termites.

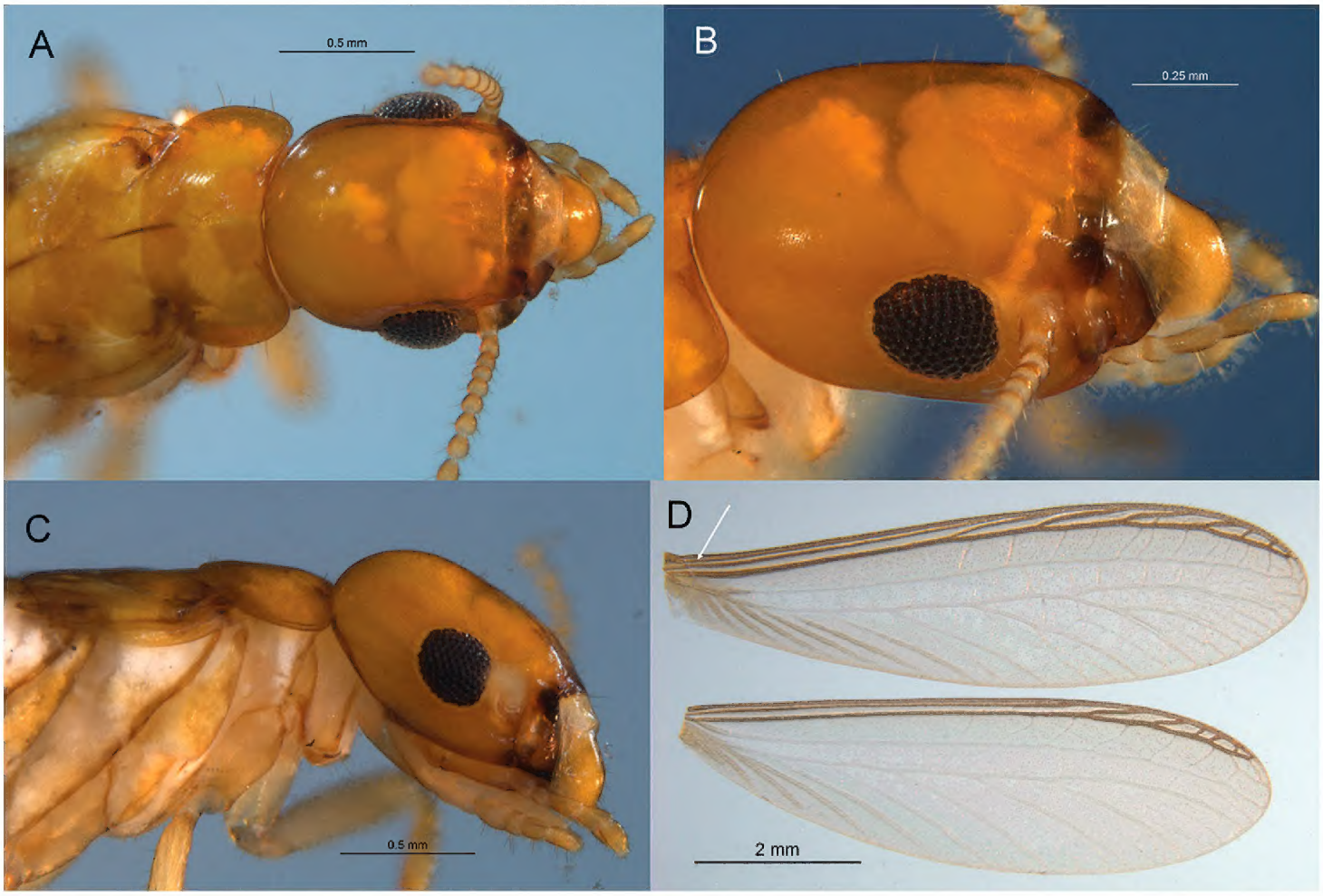

Figure 2. Imago of *Roisinitermes ebogoensis* gen. & sp. n. **A** Dorsal view of head and thorax **B** Oblique view of head **C** Lateral view of head and thorax **D** Right forewing (arrow on subcosta) and right hind wing.

***Roisinitermes ebogoensis* Scheffrahn, sp. n.**
http://zoobank.org/129573FB-E5DE-4673-9E1B-EF062D413FEB

Material examined. ***Holotype.*** Soldier from colony UF no. AFR3327. CAMEROON: Ebogo II, (+3.37723N, +11.46135E), 647 m elev., 18FEB18, col. Raphael Onana, AFR3327 ca. 500 alates, 50 soldiers, and many pseudergates, nymphs, larvae, and eggs. ***Paratypes***. CAMEROON, Ebogo II (+3.38273N, +11.46190E), 664 m elev., 10DEC2016, col. Jan Šobotník and collaborators, AFR2982 4 soldiers (1 damaged), one female dealate, and 46 brachypterous nymphs.

Diagnosis. See generic diagnosis above.

Description. ***Winged Imago*** (Figure 2, Table 1) Head and pronotum light brownish orange; eye ovoid, anterior margin truncate abdominal tergites lighter, concolorous with legs and labrum; postclypeus nearly hyaline. Compound eyes black, of medium size and protrusion; ellipsoid but truncated near antennal socket, composed of approximately 85 facets. Ocelli not visible either by pigmentation or cuticular protrusion. Antennae with more than nine articles; formula 1>2=3=4<5. Pronotum width twice that of median length; several long and shorter setae project from lateral margins. Fore wing scale with basal origins of all major veins; wing membrane covered with papillae. Tibial spurs 3:3:3; tarsi without arolia.

Soldier (Figs 4–6; Table 2) Monomorphic. In dorsal view, head capsule yellowish orange in posterior grading to orange in middle and reddish brown from frons to ante-

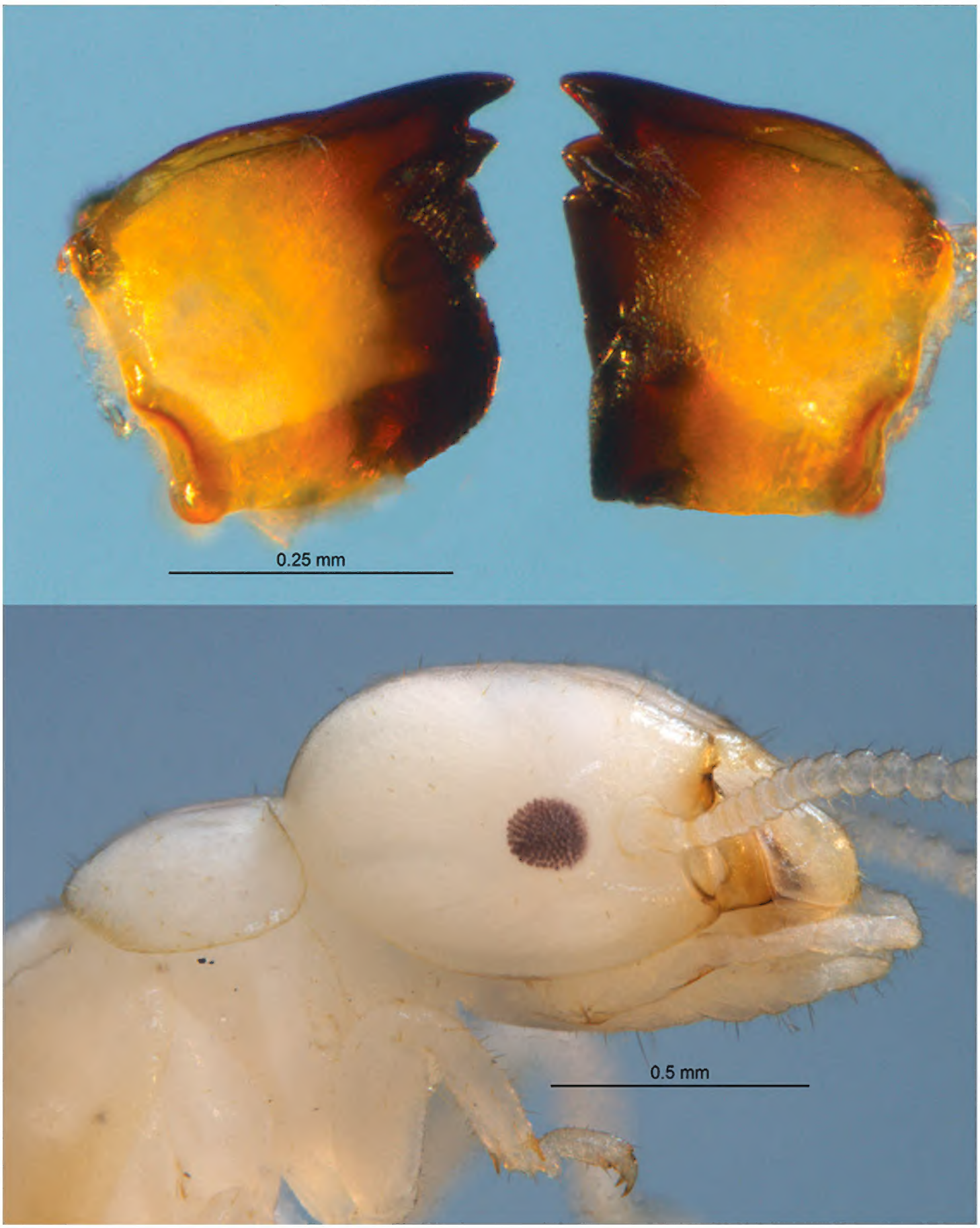

Figure 3. Brachypterous nymph of *Roisinitermes ebogoensis* gen. & sp. n. Top: Dorsal view of mandibles. Bottom: lateral view of head and thorax.

clypeus. Three proximal antennal articles sepia brown; distal articles light brown. Post clypeus and labrum yellowish with brown highlights. Eye spots prominent; large, dark brown, elliptical; formed from a mass of discrete ommatidia. Pronotum concolorous with posterior head capsule. Head capsule in dorsal view, subrectangular; lateral margins nearly parallel, length 1.5 times width. Posterior corners of head evenly rounded;

Table 1. Measurements (mm) of *Roisinitermes ebogoensis* alates from a single colony.

	Males (n=6)			Females (n=6)		
Measurement	max	min	mean	max	min	mean
Head max. width	1.05	0.95	1.00	1.05	1.00	1.03
Pronotum max. width	1.00	0.89	0.96	1.05	0.93	1.01
No. antennal articles	15	14	14.67	17.00	14.00	15.17
Max diam. eye	0.40	0.32	0.36	0.39	0.35	0.37
Body length with wings	9.63	8.63	9.10	9.88	9.50	9.65
Fore wing length (suture to tip)	7.50	6.80	7.20	7.80	7.20	7.43

Table 2. Measurements of *Roisinitermes ebogoensis* soldier (n=17 from two colonies).

Measurement	Max	Min	Mean
Head length to lateral mandible base	1.92	1.60	1.79
Head width, maximum	1.28	1.18	1.22
Head height with gula, max.	1.08	0.92	1.00
Pronotum length	0.70	0.56	0.65
Pronotum width	1.18	1.05	1.13
No. antennal articles	14	10	12.70
Left mandible width @ basal humps	0.35	0.21	0.26
Left mandible width @ middle	0.18	0.16	0.17
Max. diam. eye	0.26	0.18	0.21
Length left mandible from condyle (ventral)	1.78	1.46	1.66

posterior margin rectate. In lateral and oblique view, head capsule almost cylindrical with only slight dorso-ventral compression; frons bilobed in dorsal view, crested with rugose longitudinal stripes, rugosity lateral below frons to mandibles. In lateral view, frons sloping from vertex ~45°; mandibles bow upward to form a 15° arch. Setae short and sparse on pronotum and head capsule. Periantennal carina rugose, in dorsal view partially eclipsing the first antennal article. Small horn-like projection at terminus of ventral genae. Mandibles stick-like; long, blade narrower in middle than distal third, dentition very weak; left mandible with faint equilateral tooth approx. three fifths from base, serrations along blade from tooth to tip. Right mandible with single tooth approx. one third distance from base; blade narrowest before tooth; after tooth blade widens slightly and then gradually narrows at tip. In dorsal view, basal humps project sharply as rugose hemispheres. In lateral view, humps are columnar and equal in height to that of the mandibles. Anteclypeus shallowly incised in middle; labrum linguiform with gradual point; 4–5 long terminal setae. Antennae with 12–13 articles, third antennal article subclavate, barely shorter than fourth and fifth combined. Pronotum collar-shaped; much wider than long. Anterior margin weakly concave; lateral margins weakly convex, posterior margin forming 25° angle with incised middle. Femora moderately inflated, tibial spurs 3:3:3. Habitus as in Figure 6.

Brachypterous nymph (Fig. 3, Table 3) Body hyaline. Head, thorax, and abdomen similar in shape and pilosity of imago. Compound eyes with approx. 85 dark

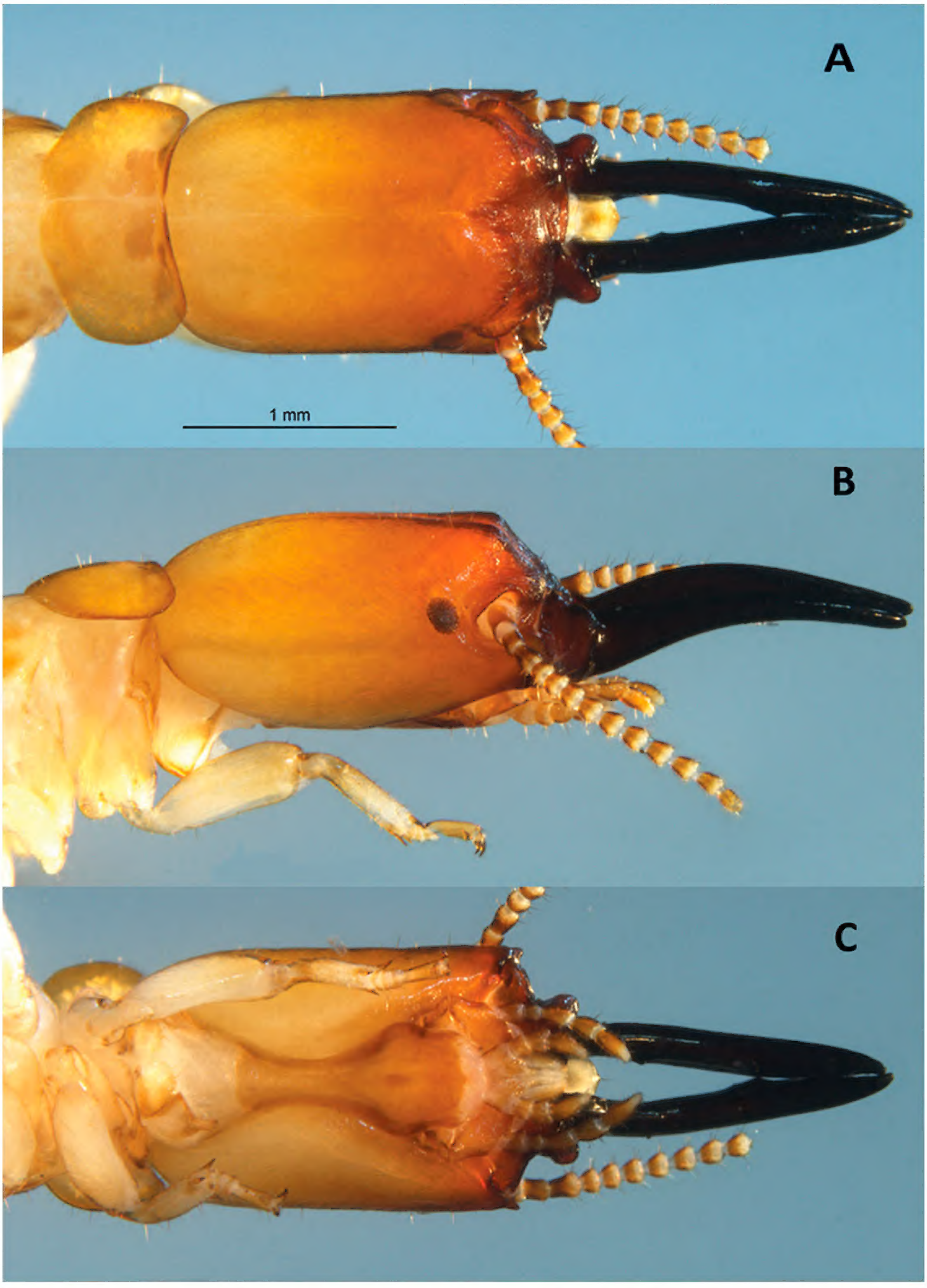

Figure 4. Soldier (holotype) of *Roisinitermes ebogoensis* gen. & sp. n. Dorsal (**A**), lateral (**B**), and ventral (**C**) views of head and pronotum.

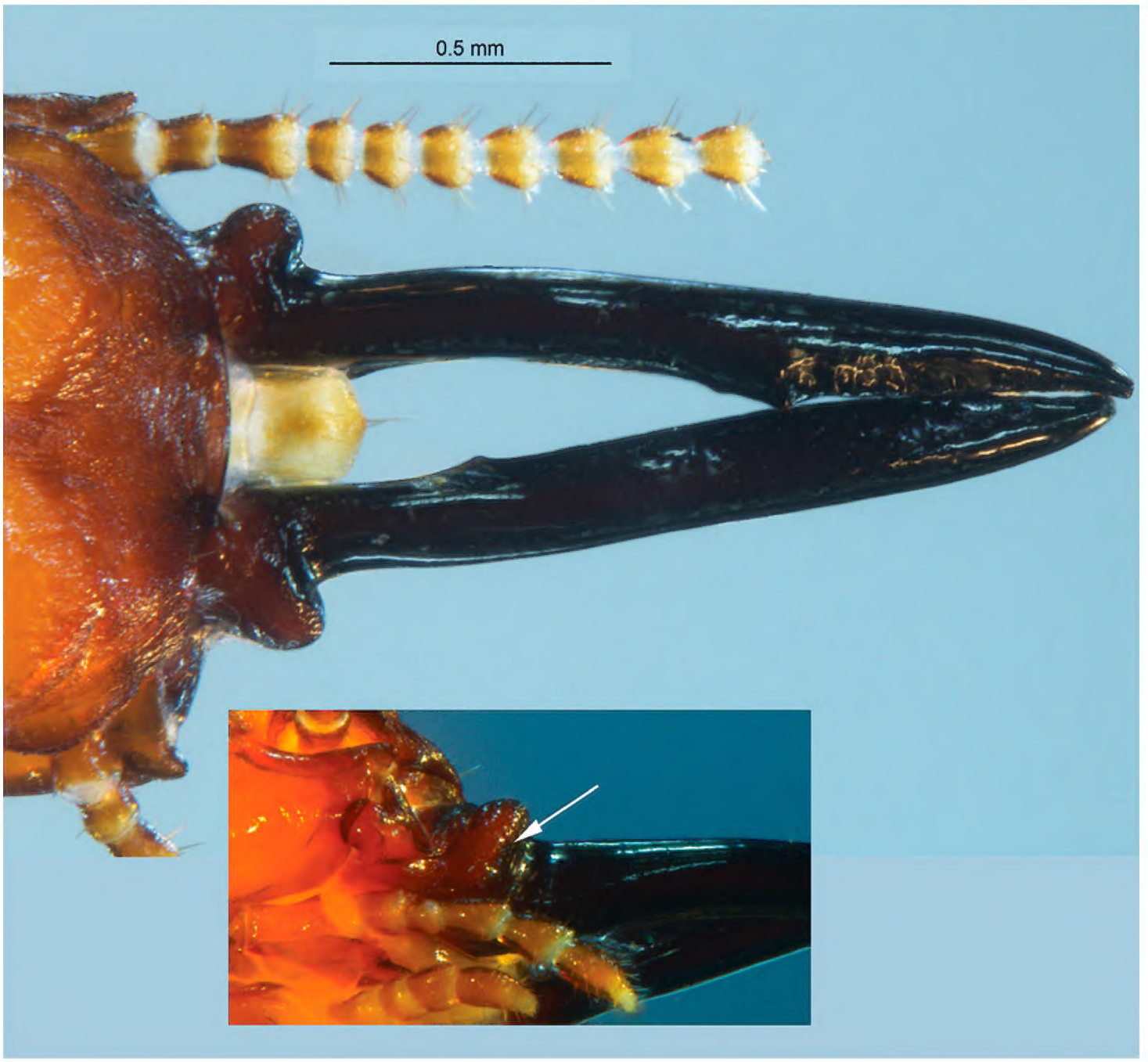

Figure 5. Dorsal view of frons and mandibles of *Roisinitermes ebogoensis* gen. n. sp. n. Inset: oblique ventral view of columnar hump (arrow).

Table 3. Measurements (mm) of *Roisinitermes ebogoensis* brachypterous nymph (n=10).

Measurement	Max	Min	Mean
Head max. width	1.10	1.00	1.07
Pronotum max. width	1.16	1.08	1.11
No. antennal articles	15	15	15
Maximum diam. eye	0.20	0.20	0.20

facets; both eyes and facets smaller than imago. Antennae with 15 articles; formula 1>2>3=4=5. Left mandible with anterior margin of marginal tooth 1.5 times longer than length of the posterior margin of the first plus second marginal tooth. Right mandible with posterior margin of second marginal tooth 1.4 times as long as molar plate.

Biology and distribution. The type colony of *R. ebogoensis* was collected in the forest on an island in the Nyong River near the Ebogo II village. The colony lived in a

Figure 6. Live habitus of soldier and brachypterous nymphs of *Roisinitermes ebogoensis* gen.et sp. n.

relatively thin (3 cm) and long (over 3 m) broad-leaf tree branch suspended from the canopy approximately 2 m above the ground. The colony contained roughly 2,000 members. A second colony of *R. ebogoensis* was collected in a nearly pristine rain forest near the village of Ebogo II. The colony was taken from a dead liana branch (ca. 15 mm diam.) hanging from the canopy at a height of approx. 1 m above the ground. Liana stems have been generally overlooked as a colonization site for Kalotermitidae (Scheffrahn et al. 2018). In light of Emerson's 1925 description of *Cryptotermes cubiceps* from a single soldier collected from a dead liana, this host should be probed routinely as a colonization site for kalotermitids.

Etymology. The species is named for the village of Ebogo II, the type locality for this termite.

Discussion

Kalotermitids inhabit a single woody item and are largely unable to move to a new food source once the original is exhausted. The lone exception is *Paraneotermes simplicicornis* that builds underground galleries connecting several wood pieces (Light 1937). The ability to feed on sound wood represents a defensive adaptation in itself as the hard food source acts as an efficient physical barrier against intruders. Kalotermitids thus show low soldier-to-worker ratios (see Haverty 1977) and soldiers reach a high level of polymorphism, reflected especially in the development of the headcap-

sule and mandibles. Some genera such as *Bicornitermes*, *Cryptotermes*, *Eucryptotermes*, *Calcaritermes*, or *Glyptotermes*, possess very short mandibles and a plug-like headcapsule to prevent intruder entry into a nest gallery (phragmosis). In *C. cryptognathus* from Jamaica, the mandibles are reduced to small stubs that do not project beyond the frontogenal boundaries of the head capsule, and therefore cannot be used to bite opponents (Scheffrahn et al. 1998). Some other genera (e.g., *Bifiditermes*, *Epicalotermes*, *Incisitermes*, *Kalotermes*, *Neotermes*) possess long mandibles with robust dentition (crushing mandibles *sensu* Prestwich 1984) used to injure an opponent mechanically. This is often combined with release of defensive secretions originating in the labial glands (Šobotník et al. 2010, Sillam-Dussès et al. 2012). *Epicalotermes pakistanicus* has particularly long and serrated mandibles (Akhtar 1974). The defensive strategy of *Roisinitermes* soldiers does not match any of these; instead, *Roisinitermes* employs a unique strategy of snapping, achieved by long and slender mandibles pressed against each other in a defensive encounter. When this potential energy is released, the left mandible springs over the right and the resultant snap is forced onto the opponent if it is in the path of the strike. This singular mandibular modification was previously known in several lineages of Termitinae (Deligne et al. 1981, Prestwich 1984, Seid et al. 2008), and was portrayed as a defensive strategy unique to this group. *Roisinitermes* represents the first undisputable evidence of parallel evolution of snapping soldiers.

Our phylogenetic analyses consistently placed *Roisinitermes* on a long branch, next to *N. insularis*. *Neotermes insularis* is a large termite species from Northern Australia with soldiers endowed with biting mandibles of crushing type. The smaller *Roisinitermes* shares no obvious similarity with *N. insularis*, supporting its generic status. Currently, the number of mitochondrial genomes available for Kalotermitidae is limited to a handful of genera, and there is a possibility that future phylogenetic analyses will support affinities between *Roisinitermes* and yet-to-be sampled taxa. In any case, the highly unusual morphology of *Roisinitermes* suggests that it shares no close relatives among modern Kalotermitidae. Future studies should focus on whether the mechanisms used by soldiers of *Roisinitermes* to snap are like those of the distantly related Termitinae.

Acknowledgements

The authors thank Eliška Cintulová, Crystal Clitheroe and Barbora Křížková for assistance on *R. ebogoensis* full mitochondrial genome sequencing. J.Š. is grateful to Ebogo II inhabitants for their help during the fieldwork, and for helping saving the Ebogo forest for future generations. J.Š. and D.S.-D. thank Aleš Buček, František Jůna, and Margot Archambeu for their hard work during the field campaigns. The field work was supported by the Czech Science Foundation (project no. 16-05318S), by the Internal Grant Agency of Faculty of Forestry and Wood Sciences, CULS (IGA No. A_27_18) and by the Grand Agency of the Czech University of Life Sciences (CIGA No. 20184307).

References

Abe T (1987) Evolution of life types in termites. In: Kawano S, Connell JJH, Hidaka T (Eds) Evolution and coadaptation in biotic communities. University of Tokyo Press, Tokyo, 125–148.

Akhtar MS (1974) New termites from Pakistan. Biologia (Lahore) 20: 23–61.

Bankevich A, Nurk S, Antipov D, Gurevich AA, Dvorkin M, Kulikov AS, Lesin VM, Nikolenko SI, Pham S, Prjibelski AD, Pyshkin AV, Sirotkin AV, Vyahh N, Tesler G, Alekseyev MA, Pavel AP (2012) SPAdes: A new genome assembly algorithm and its applications to single-cell sequencing. Journal of Computational Biology 19: 455–477. http://dx.doi.org/10.1089/cmb.2012.0021

Bourguignon T, Lo N, Cameron SL, Šobotník J, Hayashi Y, Shigenobu S, Watanabe D, Roisin Y, Miura T, Evans TA (2015) The evolutionary history of termites as inferred from 66 mitochondrial genomes. Molecular Biology and Evolution 32: 406–421. http://dx.doi.org/10.1093/molbev/msu308

Bourguignon T, Lo N, Šobotník J, Sillam-Dussès D, Roisin Y, Evans TA (2016) Oceanic dispersal, vicariance and human introduction shaped the modern distribution of the termites *Reticulitermes*, *Heterotermes* and *Coptotermes*. Proceedings of the Royal Society B-Biological Sciences 283: 20160179.

Bourguignon T, Lo N, Šobotník J, Ho SY, Iqbal N, Coissac E, Lee M, Jendryka MM, Sillam-Dussès D, Křížková B, Roisin Y, Evans TA (2017) Mitochondrial phylogenomics resolves the global spread of higher termites, ecosystem engineers of the tropics. Molecular Biology and Evolution 34: 589–597. http://dx.doi.org/10.1093/molbev/msw253

Cameron SL, Lo N, Bourguignon T, Svenson GJ, Evans TA (2012) A mitochondrial genome phylogeny of termites (Blattodea: Termitoidae): robust support for interfamilial relationships and molecular synapomorphies define major clades. Molecular Phylogenetics and Evolution 65: 163–173. http://dx.doi.org/10.1016/j.ympev.2012.05.034

Constantino R (2002) The pest termites of South America: taxonomy, distribution and status. Journal of Applied Entomology 126: 355–365. http://dx.doi.org/10.1046/j.1439-0418.2002.00670.x

Deligne J, Quennedey A, Blum MS (1981) The enemies and defense mechanisms of termites. In: Hermann HR (Ed.) Social Insects, vol 2. Academic Press, New York, 1–76.

Eggleton P, Bignell DE, Sands WA, Mawdsley NA, Lawton JH, Wood TG, Bignell NC (1996) The diversity, abundance and biomass of termites under differing levels of disturbance in the Mbalmayo Forest Reserve, southern Cameroon. Philosophical Transaction of the Royal Society B-Biological Sciences 351: 51–68. http://dx.doi.org/10.1098/rstb.1996.0004

Emerson AE (1925) The termites of Kartabo, Bartica District, British Guiana. Zoologica (New York) 6: 291–459.

Engel MS, Grimaldi DA, Krishna K (2009) Termites (Isoptera): their phylogeny, classification, and rise to ecological dominance. American Museum Novitates no. 3650: 1–27. http://dx.doi.org/10.1206/651.1

Ghesini S, Simon D, Marini M (2014) *Kalotermes sinaicus* Kemner (Isoptera, Kalotermitidae): new morphological and genetic evidence, and assignment to the new genus *Longicaputermes* gen. nov. Insectes Sociaux 61: 123–131. http://dx.doi.org/10.1007/s00040-013-0335-1

Haverty MI (1977) The proportion of soldiers in termite colonies: a list and a bibliography (Isoptera). Sociobiology 2: 199–216.

James ER, Burki F, Harper JT, Scheffrahn RH, Keeling PJ (2013) Molecular characterization of parabasalian symbionts *Coronympha clevelandii* and *Trichonympha subquasilla* from the Hawaiian lowland tree termite *Incisitermes immigrans*. Journal of Eukaryotic Microbiology 60: 313–316. https://doi.org/10.1111/jeu.12027

Inward DJG, Vogler AP, Eggleton P (2007) A comprehensive phylogenetic analysis of termites (Isoptera) illuminates key aspects of their evolutionary biology. Molecular Phylogenetics and Evolution 44: 953–967. http://dx.doi.org/10.1016/j.ympev.2007.05.014

Krishna K (1961) A generic revision and phylogenetic study of the family Kalotermitidae (Isoptera). Bulletin of the American Museum of Natural History 122: 303–408.

Krishna K (1962) New species of the genera *Allotermes* Wasmann, *Bicornitermes* Krishna, *Epicalotermes* Silvestri, and *Procryptotermes* Holmgren (Isoptera: Kalotermitidae). American Museum Novitates no. 2119: 1–25.

Krishna K, Grimaldi DA, Krishna V, Engel MS (2013) Treatise on the Isoptera of the World: Vol 1. Introduction. Bulletin of the American Museum of Natural History 377: 1–200. http://dx.doi.org/10.1206/377.1

Kück P, Meusemann K (2010) FASconCAT: Convenient handling of data matrices. Molecular Phylogenetics and Evolution 56: 1115–1118. http://dx.doi.org/10.1016/j.ympev.2010.04.024

Levings SC, Adams EA (1984) Intra- and interspecific territoriality in *Nasutitermes* (Isoptera: Termitidae) in a Panamanian mangrove forest. Journal of Animal Ecology 53: 705–714. https://doi.org/10.2307/4653

Liao Y, Chen H, Lu S, Xie Y, Zhang D (2018) The complete mitochondrial genome of drywood termite, *Incisitermes minor* (Isoptera: Kalotermitidae). Mitochondrial DNA Part B Resources 3: 324–325. http://dx.doi.org/10.1080/23802359.2017.1422397

Light SF (1937) Contributions to the biology and taxonomy of *Kalotermes* (*Paraneotermes*) *simplicicornis* Banks (Isoptera). University of California Publications in Entomology 6: 423–463.

Martius C (1994) Diversity and ecology of termites in Amazonian forests. Pedobiologia 38: 407–428.

Prestwich GD (1984) Defense mechanisms of termites. Annual Review of Entomology 29: 201–232. https://doi.org/10.1146/annurev.en.29.010184.001221

Rambaut A, Drummond AJ (2007) Tracer. http://www.beast.bio.ed.ac.uk/Tracer

Roisin Y (2000) Diversity and evolution of caste patterns. In: Abe T, Bignell DE, Higashi M (Eds) Termites: Evolution, Sociality, Symbioses, Ecology. Kluwer Academic Publishers, Dordrecht, Netherlands, 95–119. http://dx.doi.org/10.1007/978-94-017-3223-9_5

Ronquist F, Teslenko M, van der Mark P, Ayres DL, Darling A, Höhna S, Larget B, Liu Suchard MA, Huelsenbeck JP (2012) MrBayes 3.2: efficient Bayesian phylogenetic inference and model choice across a large model space. Systematic Biology 61: 539–542. http://dx.doi.org/10.1093/sysbio/sys029

Scheffrahn RH, Postle A (2013) New termite species and newly recorded genus for Australia: *Marginitermes absitus* (Isoptera: Kalotermitidae). Austral Entomology 52: 199–205. https://doi.org/10.1111/aen.12023

Scheffrahn RH, Chase JA, Mangold JR, Hochmair HH (2018) Relative occurrence of the family Kalotermitidae (Isoptera) under different termite sampling methods. Sociobiology 65: 88–100. http://dx.doi.org/10.13102/sociobiology.v65i1.2097

Scheffrahn RH, Křeček J, Ripa R, Luppichini P (2009) Endemic origin and vast anthropogenic dispersal of the West Indian drywood termite. Biological Invasions 11: 787–799. http://dx.doi.org/10.1007/s10530-008-9293-3

Scheffrahn RH, Křeček J, Su NY, Roisin Y, Chase JA, Mangold JR (1998) Extreme mandible alteration and cephalic phragmosis in a drywood termite soldier (Isoptera: Kalotermitidae: *Cryptotermes*) from Jamaica. Florida Entomologist 81: 238–240. http://dx.doi.org/10.2307/3496093

Seid MA, Scheffrahn RH, Niven JE (2008) The rapid mandible strike of a termite soldier. Current Biology 18: R1049–R1050. http://dx.doi.org/10.1016/j.cub.2008.09.033

Sillam-Dussès D, Krasulová J, Vrkoslav V, Pytelková J, Cvačka J, Kutalová K, Bourguignon, T, Miura T, Šobotník J (2012) Comparative study of the labial glands secretion in termites (Isoptera). PLoS ONE 7: e46431. http://dx.doi.org/10.1371/journal.pone.0046431

Stamatakis A, Hoover P, Rougemont J (2008) A rapid bootstrap algorithm for the RAxML Web servers. Systematic Biology 57: 758–771. http://dx.doi.org/10.1080/10635150802429642

Su NY, Scheffrahn RH (2000) Termites as pests of buildings. In: Abe Y, Bignell DE, Higashi T (Eds) Termites: evolution, sociality, symbioses, ecology. Springer, Netherlands, 437–453. http://dx.doi.org/10.1007/978-94-017-3223-9_20

Suyama M, Torrents D, Bork P (2006) PAL2NAL: Robust conversion of protein sequence alignments into the corresponding codon alignments. Nucleic Acids Research 34: 609–612. http://dx.doi.org/10.1093/nar/gkl315

Šobotník J, Jirošová A, Hanus R (2010) Chemical warfare in termites. Journal of Insect Physiology 56: 1012–1021. https://doi.org/10.1016/j.jinsphys.2010.02.012

Thorne BL, Haverty MI (1991) A review of intracolony, intraspecific, and interspecific agonism in termites. Sociobiology 19: 115–145.

Yasuda I, Kinjo K, Yaga S (2003) A new record of *Incisitermes minor* (Hagen) from Okinawa Island. Japanese Journal of Entomology New Series 6: 103–104.

Supplementary material I

Table S1

Authors: Rudolf H. Scheffrahn, Thomas Bourguignon, Pierre Dieudonné Akama, David Sillam-Dussès, Jan Šobotník

Data type: molecular data

Explanation note: Sources and GenBank accession numbers of mitochondrial sequences used for Fig. 1.

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Link: https://doi.org/10.3897/zookeys.787.28195.suppl1